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Ratite and ungulate preferences for woody New Zealand plants: influence of chemical and physical traits

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Abstract: Ratites (ostriches *Struthio camelus*) and ungulates (red deer *Cervus elaphus scoticus* and goats *Capra hircus*) were presented with 14 indigenous shrubs in cafeteria-style trials. The shrubs represented the spectrum of woody plant architecture, ranging from broadleaved monopodial species through to small-leaved highly branched divaricates. Trials were stopped when almost all shoots of the plant expected to be most preferred had been consumed. There were considerable differences between the herbivores in their selection of certain plant species. *Aristotelia fruticosa* was avoided by deer, neutrally selected by goats, and preferred by ostriches. All herbivores strongly avoided two species,

Pseudopanax crassifolius and *Coprosma rugosa.* Analysis of relative offtake (proportion of biomass consumed from each species, relative to total biomass consumed) showed that all three herbivores ate less of species with small leaves. Consumption by all herbivores was reduced by structural plant traits (i.e. divarication and related attributes) more than by chemical plant traits. The immediate impact of browsing on the plants, measured as the rank of proportion of shoots eaten, was broadly similar across the herbivores. The broadleaved species (e.g. *Myrsine australis, Aristotelia serrata*) experienced the greatest browsing, while divaricate (e.g. *Coprosma rugosa*) and conifer species (e.g. *Podocarpus hallii*) were generally least browsed. Although cafeteria-style experiments have limitations, our results for deer broadly correspond to those of field-based diet preference studies.

Keywords: browsing preferences; *Capra hircus*; *Cervus elaphus scoticus*; diet; divaricating shrubs; *Struthio camelus*

Introduction

There has been a marked shift in vertebrate herbivore guilds in New Zealand, dominated before the 17th century by indigenous flightless ratites (Holdaway & Jacomb 2000) and since replaced in the mid-19th century by a range of introduced mammals associated with

European settlement (King 2005). The ecosystem impacts of this change in vertebrate herbivore species composition and feeding mode have been the subject of much debate (e.g. Caughley 1989). The discussion has focused on the presence of distinctive herbivore-resistant features within the New Zealand flora, specifically the occurrence of divaricate species, shrubs and small trees with wide-angle branching, long internodes, and small leaves (Greenwood & Atkinson 1977). These characteristics have been variously interpreted as adaptations either to deter moa feeding (Atkinson & Greenwood 1989) or to endure aspects of climate (McGlone & Webb 1981; McGlone & Clarkson 1993). The controversy has been part of a broader discussion on the general vulnerability of the woody flora to mammalian browsing, particularly the impacts of introduced deer and goats on indigenous forests (Caughley 1983).

Bond et al. (2004) used living ratites as surrogates for the extinct moa to clarify the functional adaptations plants would require to significantly deter ratite browsing. The birds, domestic ostrich (*Struthio camelus*) and emu (*Dromaius novaehollandiae*), fed primarily by clamping and tugging on shoots. Bond et al. (2004) demonstrated experimentally that thin, strong, highly branched stems with small widely-spaced leaves reduced offtake by birds to the extent that the birds would be unable to maintain their daily energy requirements. These features are broadly characteristic of divaricate plants (Greenwood & Atkinson 1977; Kelly 1994), and especially filiramulate plants sensu Wardle & McGlone (1988). Goats, in contrast to the ratites, used their teeth and strong jaw muscles to readily consume filiramulate plants (Bond et al. 2004). These results indicate a

strong structural basis to food selection by ratites, which may not apply to mammals.

Nevertheless, both red deer (*Cervus elaphus scoticus*) and the takahe (*Porphyrio hochstetteri*), a flightless endemic rail, select within and between species of *Chionochloa* on the basis of tussock nutrient levels (Mills & Mark 1977; Mills et al. 1991). Forsyth et al. (2002) suggest that the indigenous flora has relatively neutral resistance to mammalian herbivory, based on the paucity of clearly preferred plant species across 19 studies of the preferences of deer species and goats. Although these ungulates appeared to avoid plant species with low foliar nitrogen levels, there was no significant relationship overall between diet choice and foliar nitrogen (Forsyth et al. 2002). However, Forsyth et al. (2005) demonstrated that across 21 woody species in lowland forest in Fiordland, diet selection by deer was most closely (negatively) related to foliar fibre levels, indicating a strong inhibitory effect of leaf structural components on deer feeding.

In this study we investigate further the feeding preferences of ratites and ungulates using domestic animals. Red deer, goats (*Capra hircus*), and ostrich were chosen as they represent the basic feeding types (i.e. avian, ungulate) of interest and were locally available. The aims were to determine (1) the relative influence of structural and chemical features on ratite and ungulate selection preferences, (2) whether different animal groups have similar or divergent preferences among the indigenous woody flora, and (3) the immediate impact of browsing by the different herbivores on the plants.

Methods

Fourteen native nursery-grown shrub species (Table 1), aged 2–4 years, were selected to represent a range of life forms, with one divaricating and one non-divaricating species from each of five genera, plus two *Pseudopanax* and two gymnosperm species. *Pseudopanax colensoi* is non-divaricate and *P. crassifolius* defies simple classification. Due to limited availability, *Olearia virgata* var. *lineata* and *O. solandri*, both divaricating species, were used interchangeably. The animals did not show any strong differences in response to *O. lineata* and *O. solandri*; the range of offtake values for individuals of these two species lay well within the range of offtake values within other species. *Olearia* ×*macrodonta* is a widely sold hybrid between *O. ilicifolia* and *O. arborescens*. Nomenclature follows Poole & Adams (1994).

Among the test plants one individual of each species was selected at random and retained as a control. The remaining six individuals of each species were allocated randomly to either the deer trial or the ostrich trial. The trials comprised three replicates, with each replicate containing one of each of the 14 (Table 1). In the deer and ostrich trials (Table 2), the three replicates were presented to the animals simultaneously to avoid inconvenience to the stock handler. The replicates were arranged along the fence-line of a grassy paddock, with a 4-m gap between each replicate and a single pace between individual plants within replicates (Fig. 1). The position of each plant within the replicate

was allocated at random, and plant pots were pegged down with tent pegs to prevent them being knocked over.

The goat trial, which took place 2 months after the deer and ostrich trials (Table 2), utilised healthy plants left over from the other two trials. *Olearia virgata* var. *lineata* were unavailable for the goat trial, so only *O. solandri* were used. In the goat trial, the replicates were separated in time (by c. 10 min). Again, plants within replicates were arranged randomly along a fence-line.

In all trials, we aimed to use the methods described by Krebs (1989), where the trial is stopped once all of the edible material from the most palatable plant has been consumed. One individual of *Aristotelia serrata* was observed; when almost all the edible material on this individual had been consumed, the animals were removed. The deer consumed most of the shoots on the *A. serrata* individual after feeding for 10 min. The ostriches consumed most of the *A. serrata* shoots after 35 min, but some further browsing occurred on many species as it was necessary to remove the plants, not the birds, from the paddock. The goats (offered one replicate at a time) were stopped from feeding when they had consumed most of the *A. serrata* shoots after 5 min (replicate 1), 7 min (replicate 2) and 5 min (replicate 3) respectively.

Immediately before and after each feeding trial, plant height and the numbers of undamaged live shoots were recorded. A 'shoot' was defined as an external tip composed of both stem and leaf material. The number of undamaged shoots post-trial was subtracted from the pre-trial number to determine number of shoots removed.

On each plant, the clip diameter (the diameter of the stem at the point where the shoot was bitten off) was recorded five times per plant (or less if fewer than five bites had been taken). Mean clip diameters (rounded to the nearest millimetre) were calculated for each herbivore and each plant species. On the control plants, five harvests were made from each species using secateurs to cut at each herbivore's clip diameter. For example, if the mean clip diameter of deer on *Podocarpus hallii* was 2 mm and the mean clip diameter of ostriches and goats for this species was 1 mm; five harvests would be made at 2 mm and five at 1 mm. The numbers of shoots harvested were counted. All harvested material was oven-dried at 70^{o} C for 48 h, then weighed. Mean shoot mass (specific to each plant and herbivore) was calculated by dividing the mass of harvested material by the number of shoots.

Plant traits

Chemical plant traits

Samples of leaf and stem were collected from the control plants, oven-dried at 70ºC for 48 h and ground using a Cyclone sample mill (Udy Corp, Fort Collins, CO, USA). Nitrogen and phosphorus concentrations were determined using a continuous flow analyser following a modified Kjeldahl digestion (Bremner & Mulvaney 1982; Blakemore et al. 1987). Total phenolic concentration was determined using the Price & Butler (1977) method, following extraction with acetone.

Physical plant traits

Leaf width and leaf length were measured five times on one individual of each species from the control group, using the guidelines of Cornelissen et al. (2003). Leaf area was estimated by multiplying length × breadth (means of 5 leaves) × 0.67 (Kelly 1994). The tensile strength of external shoots and the diameter at which stem failure (breakage) occurred were measured five times for each species. Tensile strength was determined by clamping an excised branch into a vice and an external shoot from the branch into a vice grip attached to a dynamometer (Bond et al. 2004), and pulling slowly until stem failure occurred. If a stem broke where it was clamped, the trial was discarded. As observed by Bond et al. (2004), failures often occurred at nodes rather than internodes. On *Pseudopanax crassifolius*, the force required to pull leaves from the main stem was measured, since the individuals used did not have branches. Tensile strength measurements were expressed relative to shoot cross-sectional area, as Newtons per square millimetre (N mm^{-2}).

The divarication index (Kelly 1994) was calculated for each species using Equation 1:

$$D = \frac{(100/a)}{b} + \frac{10}{b} + \frac{c}{5}\ , \qquad (1)$$

where *D* is the divarication index, *a* is the number of leaves on 10 cm of one axis at the tip of a branch, *b* is the mean width of leaves at the branch tip, and *c* is the mean angle between side branches and the main stem on any given branch. The divarication index could not be calculated for *Pseudopanax crassifolius*, as the individuals used did not have branches.

Data analysis

Relative offtake

To estimate biomass offtake from each plant, the number of shoots removed by herbivores was multiplied by the mean shoot mass for that herbivore×plant-species combination. Offtake from each plant was expressed as a proportion of total offtake from all species in the replicate (Eqn 2):

$$P_1 = \frac{x_1}{\sum(x_1 + x_2 + \ldots x_n)}, \qquad (2)$$

where P_1 is the proportion of total biomass offtake for plant 1, x is the biomass offtake from an individual plant and n is the number of plants in the replicate. *P*, the relative proportion of total biomass offtake, was transformed by taking natural logs $[\ln((P \times 100)+1)]$ to improve the normality of the data, giving *ln (P)*, described from here on as 'relative offtake'.

Comparison of herbivore preferences for individual plant species

To determine whether the different herbivores had significantly different preferences, two-way analysis of variance with randomised blocks (ANOVA; GenStat 2002) was run on relative offtake (*ln (P)*), including effects for plant species, herbivore, and for the interaction plant-species×herbivore. The blocking factor was replicate.

Variables predicting preferences

Principal components analysis (PCA; GenStat 2002) was performed on all the plant trait variables. Only seven plant traits, which were not strongly correlated with each other and that represented the full range of variables of interest (Table 3), were included in further analyses.

Since *Pseudopanax crassifolius* did not have a divarication index, two datasets were generated and analysed separately. The first excluded *P. crassifolius* from the calculation of relative offtake, and retained all seven possible explanatory variables (Table 3). The second included *P. crassifolius* but excluded divarication index from the possible explanatory variables. Multiple linear regression was carried out on each dataset for each herbivore, and backward stepwise selection was performed to identify the minimal combination of chemical and physical plant traits predicting selection preferences for each herbivore (McCullagh & Nelder 1989; GenStat 2002). The response variable in each case

was *ln (P)*. To determine the relative importance of the variables in the minimal models, each was used in turn as the sole explanatory term.

Proportion of shoots browsed

The proportion of shoots browsed on individual plants was calculated by dividing the number of shoots removed by the initial number of shoots; these data provide information on the impact of browsing. Due to the differences in numbers of animals and length of grazing trials, the data can only be used as ranks. Data from the three replicates were averaged, and plant species ranks calculated for each herbivore. Spearman rank correlation coefficients (r_s) were calculated for each herbivore pair.

Results

Comparison of herbivore preferences for individual plant species

The pattern of offtake within herbivores was generally that the non-divaricating species of the plant genus pairs were eaten more than the divaricating species (Fig. 2). Exceptions were the genera *Aristotelia* and *Sophora* (ostriches), and *Myrsine* (goats) (Fig. 2). All three herbivores avoided *Pseudopanax crassifolius* and *Coprosma rugosa*, and selected *Aristotelia serrata*. Deer and ostriches selected for *Myrsine australis*, and goats selected for *Coprosma chathamica* (Fig. 2). *Aristotelia fruticosa* was avoided by deer, weakly selected by goats, and preferred by ostriches (Fig. 2; ANOVA, $F_{2,8} = 14.8$, $P < 0.01$). Both *Aristotelia serrata* ($F_{2,8} = 9.1$, $P < 0.05$) and *Pseudopanax colensoi* ($F_{2,8} = 10.6$, $P < 0.05$) were selected by deer more than by ostriches. Goats selected less *Prumnopitys ferruginea* than the other herbivores ($F_{2,8} = 6.6$, $P < 0.05$).

Ostriches showed strong selection for two divaricating species, *Aristotelia fruticosa* and *Myrsine divaricata*. *A. fruticosa* has a relatively low divarication index, which may explain its selection by ostriches. However, *M. divaricata*, which was also strongly selected by goats and was the most preferred of the divaricating species by deer, has a divarication index close to the average for divaricating species (Table 3).

Using relative offtake (*ln (P)*) as the response variable (i.e. offtake from each plant relative to total offtake from the replicate) allowed direct comparison of the preferences of

the three herbivore species, despite the variation in numbers of animals and lengths of feeding trials.

Variables predicting relative offtake by herbivores (*P. crassifolius* excluded)

The minimal model (i.e. the model providing the best fit to the data using as small a number of terms as possible) for deer included the terms square-root leaf area and stem strength (Table 4), suggesting that deer selected for large leaves and weak stems. When each of the explanatory variables was included in the model as a sole term (results not shown), stem strength explained the greatest amount of variation. Plants selected by goats had a low divarication index and large leaves (Table 4), with leaf size being the most important sole term. Plants selected by ostriches had a low divarication index and high stem phenolics, with divarication index being the most important sole term.

Each plant species was excluded from the model in turn to check whether it was having undue effect on the terms included in the minimal model, or on the slope direction (positive/negative) of the parameter estimates. For ostriches, the minimal models always included divarication index (negative slope) and stem phenolics (positive slope). Only the exclusion of *Coprosma chathamica* influenced the terms in the minimal model, with leaf phosphorus also included (positive slope). For goats, the terms divarication index (negative slope) and square-root leaf area (positive slope) were always included in the minimal model, except when *Aristotelia serrata* was excluded, when either term but not

both were significant. For goats, exclusion of a number of species (*Coprosma chathamica*, *C. rugosa*, *Myrsine australis*, *Olearia macrodonta* and *Podocarpus hallii*) resulted in the term stem phenolics being included in the minimal model, with a positive slope. For deer, shoot strength and square-root leaf area were always included in the minimal model, except when *Aristotelia serrata* was excluded, when either term but not both could be included. When *Pseudopanax colensoi* was excluded, a number of other terms became significant: stem nitrogen (negative slope); leaf phosphorus (positive slope); divarication index (negative slope). These results demonstrate that the minimal models presented for the three herbivores are robust.

Variables predicting relative offtake by herbivores (*P. crassifolius* included)

Analysis of all species, with divarication index omitted from the list of potential explanatory variables, had almost no effect on the minimal model for deer (Tables 4 and 5). For goats and ostriches, the new minimal model included the terms stem phenolics and square-root leaf area (Table 5). Leaf size (Fig. 3) appeared to be a predictor of relative offtake for all three herbivores.

Proportion of shoots browsed – impacts on plants

The proportion of shoots browsed indicates the immediate severity of impact that browsing has on a plant. It is necessary to interpret these results carefully, since overall, the ostriches consumed more material than the deer or goats. However, the plant species rankings for the different herbivores (Table 6) provide useful information on the immediate impact of browsing on these plant species.

The impact of browsing was similar for many of the species across herbivores, with three of the four plant species experiencing the greatest browsing damage being the same for all herbivores: *Myrsine australis*, *Aristotelia serrata* and *Olearia* ×*macrodonta*. *Pseudopanax colensoi* occurred in the top four for deer, while *Coprosma chathamica* was among the top four for ostriches and goats. For all herbivores, two of the four plant species with the least browsing damage were *Coprosma rugosa* and *Pseudopanax crassifolius*.

The ranks of impact were strongly significantly correlated between the herbivores: Spearman rank correlation coefficients (r_s, 12 d.f.) were 0.67 between deer and ostrich ($P < 0.01$), 0.70 between deer and goats ($P < 0.01$), and 0.88 between ostriches and goats ($P < 0.001$).

Discussion

Short-term, cafeteria-style, preference experiments are clearly unable to address the complexities of herbivory in natural environments (Perez-Harguindeguy et al. 2003). The results have to be used with caution when making direct comparisons between herbivores, as groups of animals in a preference trial can influence the feeding performance of individuals through dominance behaviour (Barroso et al. 2000), though this was not evident during the experiments from casual observation. The use of juvenile nursery-grown plants is also a limitation, as they may not adequately represent the chemical and structural features of the species concerned in natural communities. For example, the divarication index for the three species in common (*Aristotelia fruticosa*, *Coprosma rugosa*, and *Myrsine divaricata*) were between 20 and 30% higher in populations at Lewis Pass (Kelly 1994) compared with the experimental plants used in this study. The foliar and stem nutrient levels of the nursery-grown shrubs may be higher than those of plants found in natural ecosystems. The final, and possibly most important, caveat is the use of domestic animals, raised on pasture (*Lolium perenne*, *Trifolium repens*) and food supplements and therefore relatively naïve about the indigenous woody species presented to them (Provenza et al. 2003). This is especially the case for the ostriches, which had no prior opportunity to eat any of the shrubs presented to them in this trial (Table 2).

However, the relative offtake by deer from woody angiosperms in this study matches general browse assessments and field-based diet studies. The ranking of preferred

(*Myrsine australis, Aristotelia serrata, Pseudopanax colensoi*) and selection-neutral (*Sophora microphylla*, *M. divaricata*) trees and shrubs listed for deer by Forsyth et al. (2002) are similar to the rankings obtained in our study (Fig. 2). The two exceptions are *Pseudopanax crassifolius*, which was listed as preferred by Forsyth et al. (2002) but avoided by all three herbivores in our study, and *Olearia* ×*macrodonta*, which was eaten in our study but listed as avoided by these authors. Interestingly, both species have foliage with marginal sharp projections that may initially at least deter herbivores.

Our results for selection by deer of gymnosperms (moderate for *Prumnopitys ferruginea* and neutral for *Podocarpus hallii*) contrast with those of Forsyth et al. (2002), who found both plant species to be avoided. Although not a significant term in the minimal model, stem phenolics may be influencing deer choice between these two species: *Podocarpus hallii* has considerably greater leaf and stem phenolics than *Prumnopitys ferruginea*. Vourc'h et al. (2002) found that consumption of western red cedar by Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) was negatively associated with mono-terpene content, another measure of plant chemical defence.

The goats in our experiment appeared to select primarily for structure rather than nutritional quality (Table 4). In contrast, Pande et al. (2002) found that goats and sheep preferred woody legumes (e.g. *Medicago arborea, Ulex europaeus, Robinia pseudoacacia*) over non-leguminous shrubs (e.g. *Leptospermum scoparium*, *Ozothamnus leptophyllus*), a pattern that broadly corresponded to in vitro digestibility results (Lambert et al. 1989). The ostriches in our experiment appeared to select negatively for divarication

and positively for stem phenolics. In contrast, Milton et al. (1994) found that ostrich preferred forbs with low phenolics to those with high phenolics. The naïvety of these birds for native shrubs may have limited their ability to select between species on the basis of chemical defences, as taste is limited in birds (McDonald et al. 1995).

Analysis showed that several structural variables influenced herbivore selection preferences, including divarication index, leaf area and stem strength (Tables 4 and 5, Fig. 3). The only chemical trait to significantly influence selection, stem phenolics, had the opposite effect to that expected, with ostriches and goats appearing to select plants with high stem phenolics, which is unusual.

All vertebrates favoured those woody species with larger leaves, and when divarication index was included in the analysis, it was a significant term for both ostriches and goats. For deer, two variables that are related to divarication, stem strength and leaf size, were significant terms in the minimal model. Plant morphology may have a greater impact than chemical composition on herbivore selection preferences (Hartley et al. 1997), especially when herbivores are faced with novel food species.

Herbivore preferences are clearly context-dependent and will vary with age, sex, and dietary experience of the animal, as well as with the vegetation context in which the study is undertaken. Individual species preferences and the factors determining those preferences can therefore be expected to vary between studies, as has been shown by Forsyth et al. (2002, 2005).

The result from our preference experiments, that divarication and variables related to divarication such as leaf size and stem strength, apparently deter ungulates as well as ratites, differs from those obtained previously by Bond et al. (2004). They argued that divaricates were more vulnerable to ungulates than to ratites. They found that the birds' mode of feeding limited intake from plants with divaricate architecture to levels below daily maintenance requirements. However, our preference experiments did not test the functional response of herbivores, as we could not measure bite consumption rates. Further investigations are required on the impact of different herbivores on subsequent regrowth response of the grazed plants (Augustine & McNaughton 1998), with associated measures of herbivore numerical and functional responses, before we can confidently identify features of the New Zealand woody flora adapted to avian herbivory.

Conclusion

The key result of our preference experiments is that differences in feeding preferences between ratites and ungulates are less marked than expected. Both ratites (ostriches) and ungulates (deer and goats) appeared to select primarily on the basis of structure, avoiding highly divaricating species, whereas chemical plant traits had less impact on short-term selection by these herbivores. Within this broad pattern, there were marked differences in selection preferences between the herbivore species. The immediate impact of browsing, in terms of the proportion of shoots browsed, was greatest for the broadleaved species.

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Table 1. Shrub species used in ratite and ungulate feeding trials.

Family	Non-divaricates	Divaricates*	Gymnosperms/ Other
Elaeocarpaceae	*Aristotelia serrata*	*Aristotelia fruticosa*	
Rubiaceae	*Coprosma chathamica*	*Coprosma rugosa*	
Myrsinaceae	*Myrsine australis*	*Myrsine divaricata*	
Asteraceae	*Olearia ×macrodonta*	[+]*Olearia virgata* var. *lineata* / *Olearia solandri*	
Podocarpaceae			*Podocarpus hallii*
Podocarpaceae			*Prumnopitys ferruginea*
Araliaceae	*Pseudopanax colensoi*		*Pseudopanax crassifolius*
Fabaceae	*Sophora microphylla* var. *longicarinata*	*Sophora microphylla*	

* sensu Atkinson & Greenwood (1989). [+]Used interchangeably

Table 2. Deer, goat and ostrich feeding trial information.

Trial	Red deer	Ostrich	Goat
Age of animals	2 years	8–11 months	1–3 years
Sex of animals	Male	Male and female	Male and female
No. animals in trial	100	80	7
No. animals that ate during trial	c. 20	c. 80	6
Replicate method	3 replicates, separated by 4-m gap	3 replicates, separated by 4-m gap	3 replicates, separated in time (c. 10 min apart)
Duration of trial	10 min	45 min	5 min, 7 min, 5 min
Previous opportunity to eat native shrubs?	Yes	No	Yes

Table 3. Values of physical and chemical plant traits used in analysis of ratite and ungulate feeding preferences.

	Chemical			Physical			
Species	Stem N (%)	Leaf P (%)	Stem phenolics (%)	Divari-cation index	$\sqrt[2]{\text{leaf area}}$ (mm)	Stem tensile strength (N mm^{-2})	Initial ht* (cm)
Aristotelia fruticosa	0.83	0.16	7.29	15.3	7.09	28.5	71.7
Aristotelia serrata	1.73	0.25	5.56	14.8	82.70	10.4	55.7
Coprosma chathamica	2.40	0.36	2.00	8.7	23.68	26.7	44.7
Coprosma rugosa	0.65	0.21	2.01	24.2	2.48	28.8	47.7
Myrsine australis	0.83	0.16	7.14	12.1	29.53	7.7	63.3
Myrsine divaricata	1.04	0.16	5.31	17.0	11.77	16.6	58.7
Olearia virgata var. *lineata*	1.96	0.61	1.94	23.2	5.41	28.1	48.0
Olearia ×macrodonta	3.44	0.24	2.66	10.2	54.84	6.5	41.7
Olearia solandri	0.98	0.16	2.49	15.7	2.89	35.4	45.0
Podocarpus hallii	0.79	0.18	7.29	21.9	5.56	12.6	90.7
Prumnopitys ferruginea	0.85	0.28	4.32	19.8	5.00	15.3	94.7
Pseudopanax colensoi	0.33	0.06	2.30	7.7	47.91	6.1	54.0
Pseudopanax crassifolius	1.72	0.25	1.73	_	34.17	9.8	69.0

Sophora longicarinata	1.31	0.23	2.62	15.6	15.32	11.6	71.0
Sophora microphylla	1.50	0.38	2.09	19.2	15.40	39.0	86.0

*Height values here are averages; individual plant heights were used in the analysis.

Table 4. Parameter estimates of significant variables in the minimal model for each herbivore, analysed with *Pseudopanax crassifolius* excluded (response variable is relative offtake, *ln (P)*). Divarication index was included as one of the initial explanatory variables of feeding preference for each herbivore.

	Red deer			Goat			Ostrich		
Term	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Constant	2.1	0.428	<0.001	2.4	0.709	0.002	2.8	0.439	<0.001
Divarication index				−0.093	0.037	0.017	−0.124	0.024	<0.001
Stem phenolics							0.221	0.058	<0.001
$\sqrt[2]{\text{leaf area}}$	0.018	0.007	0.013	0.022	0.008	0.007			
Stem strength	−0.057	0.016	<0.001						
F statistic	$F_{2, 38} = 21.6$			$F_{2, 38} = 17.1$			$F_{2, 36} = 18.0$		
Significance	$P < 0.001$			$P < 0.001$			$P < 0.001$		
Variance accounted for:	52.0%			45.8%			48.6%		

Table 5. Parameter estimates of significant variables in the minimal model for each herbivore, analysed with all species including *Pseudopanax crassifolius*, but with divarication index omitted from the list of potential explanatory variables (response variable is relative offtake, *ln (P)*) for feeding preference.

	Red deer			Goat			Ostrich		
Term	Estimate	SE	*P*	Estimate	SE	*P*	Estimate	SE	*P*
Constant	1.8	0.489	<0.001	0.03	0.375	0.943	0.2	0.336	0.490
Stem phenolics				0.153	0.074	0.046	0.237	0.065	0.003
$\sqrt[2]{\text{leaf area}}$	0.018	0.008	0.032	0.031	0.007	<0.001	0.221	0.058	<0.001
Stem strength	–0.045	0.018	0.017						
F statistic	$F_{2, 41} = 12.6$			$F_{2, 41} = 11.9$			$F_{2, 39} = 11.1$		
Significance	$P < 0.001$			$P < 0.001$			$P < 0.001$		
Variance accounted for:	36.1%			34.7%			34.1%		

Table 6. Impact of ratite and ungulate browsing on plants: mean proportion of shoots browsed, arranged by rank. See Table 1 for genera.

	Red deer		Goat		Ostrich	
Rank	Species	Prop	Species	Prop	Species	Prop
1	*M. australis*	0.77	*A. serrata*	0.76	*O. ×macrodonta*	1.00
2	*A. serrata*	0.63	*C. chathamica*	0.73	*A. serrata*	0.98
3	*P. colensoi*	0.51	*M. australis*	0.70	*M. australis*	0.97
4	*O. ×macrodonta*	0.37	*O. ×macrodonta*	0.65	*C. chathamica*	0.93
5	*P. ferruginea*	0.27	*M. divaricata*	0.51	*M. divaricata*	0.93
6	*S. longicarinata*	0.26	*S. longicarinata*	0.31	*A. fruticosa*	0.90
7	*M. divaricata*	0.22	*P. colensoi*	0.30	*P. colensoi*	0.85
8	*C. chathamica*	0.21	*S. microphylla*	0.10	*S. longicarinata*	0.63
9	*P. hallii*	0.12	*A. fruticosa*	0.09	*P. ferruginea*	0.58
10	*S. microphylla*	0.02	*O. solandri*	0.02	*S. microphylla*	0.55
11	*O. lineata/solandri*	0.01	*P. hallii*	0.02	*P. crassifolius*	0.33
12	*C. rugosa*	0.01	*P. ferruginea*	0.01	*O. lineata/solandri*	0.32
13	*A. fruticosa*	0.01	*C. rugosa*	0.00	*P. hallii*	0.04
14	*P. crassifolius*	0.00	*P. crassifolius*	0.00	*C. rugosa*	0.00

Figures

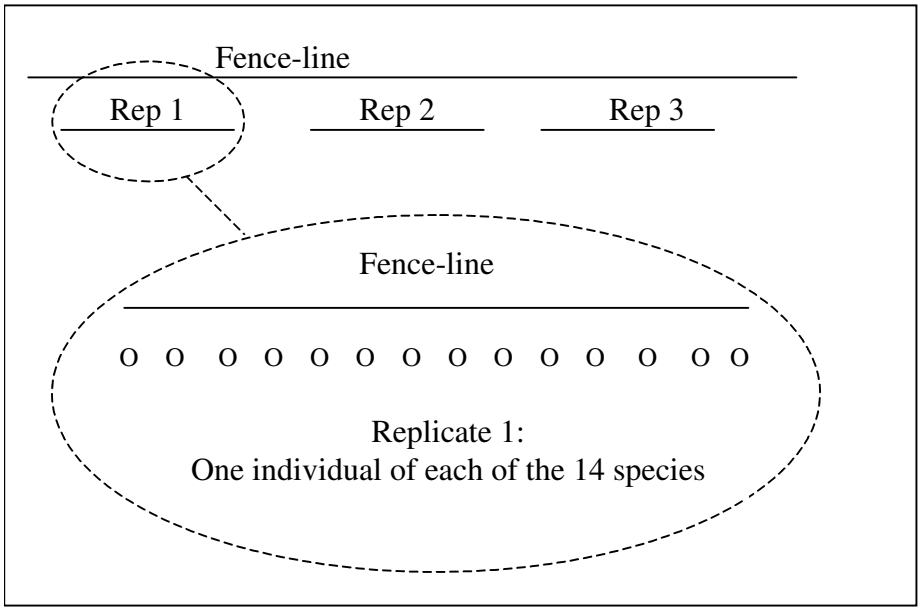

Figure 1. Layout of replicates in red deer and ostrich feeding trials.

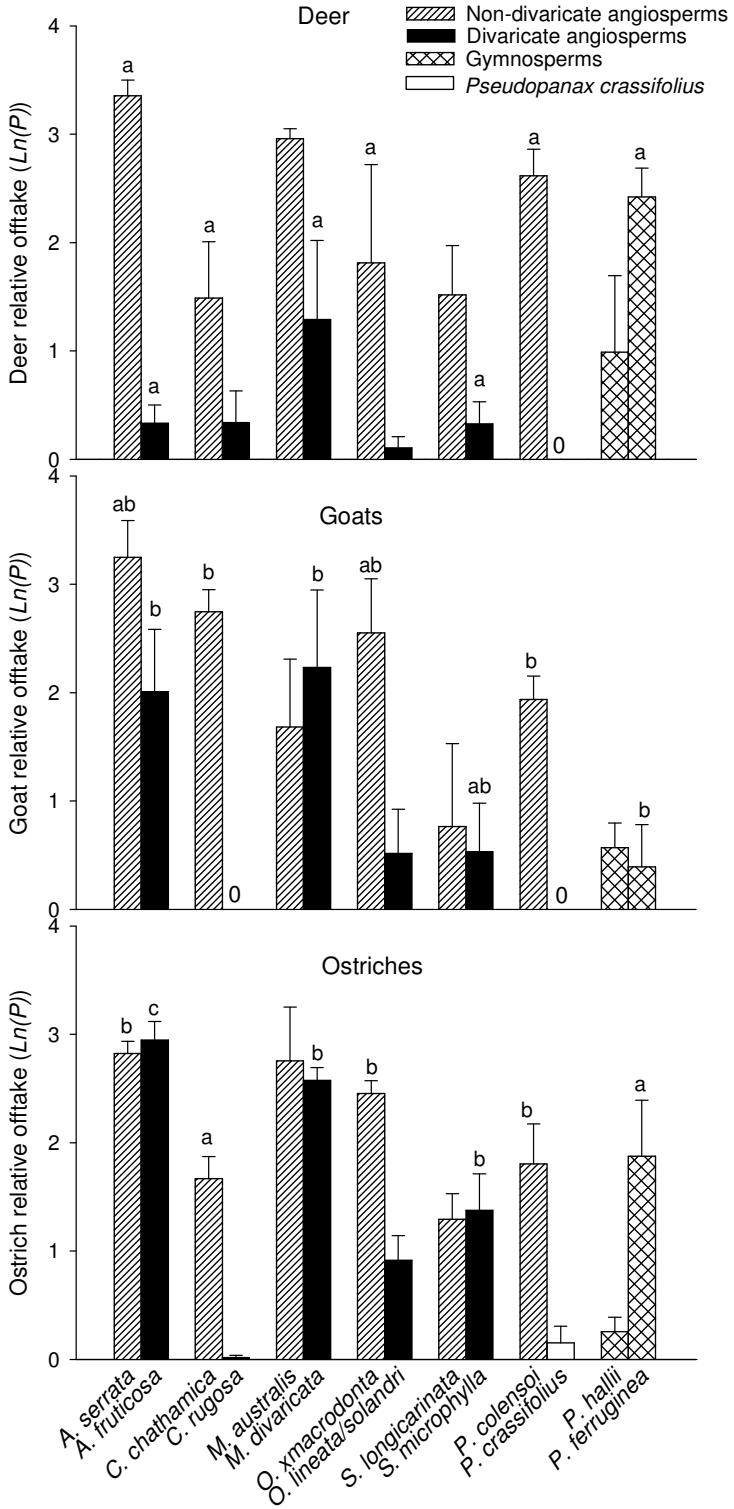
Deer
Non-divaricate angiosperms
Divaricate angiosperms
Gymnosperms
Pseudopanax crassifolius
Deer relative offtake (Ln(P))
Goats
Goat relative offtake (Ln(P))
Ostriches
Ostrich relative offtake (Ln(P))
A. serrata
A. fruticosa
C. chathamica
C. rugosa
M. australis
M. divaricata
O. xmacrodonta
O. lineata/solandri
S. longicarinata
S. microphylla
P. colensoi
P. crassifolius
P. hallii
P. ferruginea

Figure 2. Relative offtake (*ln (P)*) by red deer, goats and ostriches, with non-gymnosperm species arranged in congeneric pairs. Bars are standard error, $n = 3$ plants, different letters indicate significant difference ($P < 0.05$) between herbivores in offtake from that plant species.

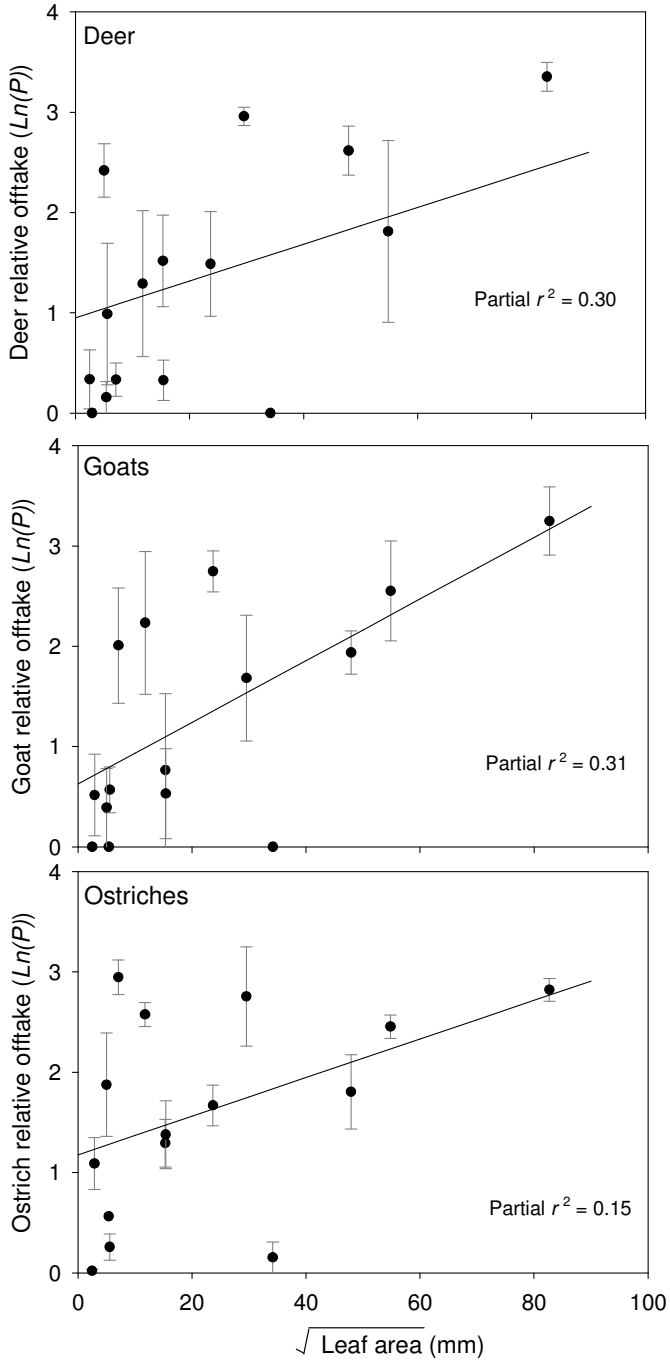

Figure 3. Relative offtake by red deer, goats and ostriches in relation to leaf area. Bars are standard error, n = 3 plants of each species, except for *Olearia solandri* and *O. virgata* var.

lineata where $n = 1$ or 2. Prediction lines generated by linear regression, using the minimal model for each herbivore; values for terms other than square-root leaf area were held constant at their average. Minimal model created for all species, with divarication index not used as an explanatory term.